

**Abstract**—The feeding habits of the Mediterranean spiderfish, *Bathypterois mediterraneus*, the most abundant fish below 1000 m on the deep slope of the Catalan Sea (western Mediterranean), were studied. Samples were obtained at depths between 1000 and 2250 m. Diet was analyzed for two different size classes (immature and mature specimens) and three different bathymetric strata. The most important food items found were benthopelagic planktonic calanoid copepods. In juveniles from 1800 to 2250 m, benthic tanaidaceans were secondary, whereas in the adults, mysids were secondary. At other depths, there were no secondary prey: calanoid copepods were consumed almost exclusively; other items were very scarce. Adults ingest larger amounts and sizes of prey than juveniles. The scarcity of resources below 1200–1400 m diversified the diet, although it still primarily consisted of elements from the benthopelagic plankton.

## Feeding ecology of the Mediterranean spiderfish, *Bathypterois mediterraneus* (Pisces: Chlorophthalmidae), on the western Mediterranean slope

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The genus *Bathypterois* Günther, 1878 comprises a small group of benthic chlorophthalmid species adapted for life in the deep sea. The genus is circumglobal at temperate latitudes (Sulak, 1984a). Two species of *Bathypterois* are found in the Mediterranean: *Bathypterois dubius* and *Bathypterois mediterraneus* (Bauchot, 1962). The presence of a third, *Bathypterois grillator*, based on underwater photographs, has been suggested by Sulak (1984a). The Mediterranean spiderfish, *Bathypterois mediterraneus*, is the only endemic species of the genus, and undoubtedly the most abundant in the Mediterranean (Sulak, 1977; Bauchot, 1987).

Some species of the genus *Bathypterois*, such as *Bathypterois dubius*, *Bathypterois grillator*, *Bathypterois atricolor*, and *Bathypterois viridensis*, have been observed from submersibles (Church, 1971; Heezen and Hollister, 1971; Saldanha, 1977; Jones and Sulak, 1990; Chave and Mundy, 1994; Chave and Malahoff, 1998). The fish are benthic, rest on the bottom, and touch the sediment with their longest pelvic and caudal rays (Heezen and Hollister, 1971; Saldanha, 1977), while the long pectoral rays are directed forwards over the head (Saldanha, 1977). Pectoral rays are likely used as sensory devices to detect the presence of planktonic prey, by both direct contact and chemoreception (Sulak, 1977).

According to Sulak (1984a), *Bathypterois mediterraneus* is benthic on the con-

tinental slope and rise, at 260–2800 m. However, in the Catalan Sea (western Mediterranean), the species is restricted in its bathymetric distribution to depths greater than 748 m (Stefanescu et al., 1992a, 1994; Morales-Nin et al., 1996). Of the 31 different species of deep-water fish in the Catalan Sea (Stefanescu et al., 1992a), *Bathypterois mediterraneus* is subdominant between 1000 and 1500 m, and dominant below this depth. At 1000–2250 m *Bathypterois mediterraneus* is the fourth in importance for biomass of all fish (Stefanescu et al., 1992a). This species aggregates (Stefanescu et al., 1992a; Morales-Nin et al., 1996), contrary to Sulak's (1984a) observation that it is usually solitary, but may aggregate occasionally.

Knowledge of the biology of deep-sea fauna in the Mediterranean is limited. The feeding habits of some deep-water fish and decapod species in the Catalan Sea have been studied recently (Cartes and Sardà, 1989; Carrassón et al., 1992; Cartes and Abelló, 1992; Cartes, 1993a, 1993b, 1993c). Information on *Bathypterois mediterraneus* biology is limited and fragmentary. Data regarding growth and depth-size trends are given by Morales-Nin (1990), Stefanescu et al. (1992b), and Morales-Nin et al. (1996). The morphological and morphometric characteristics of the alimentary tract and some generic data on the diet of this species have been reported by Carrassón and Matallanas (1990, 1994).

**Table 1**

Sampling data for *Bathypterois mediterraneus* in the present study. N lat = North latitude; E long = East longitude. *n* = number of specimens sampled.

Station	Date	Depth (m) (initial final)	Final situation		<i>n</i>
			N lat	E long	
BII-4	Jul 29 1987	1432 1419	40 44.7	1 52.6	2
BII-5	Jul 30 1987	1753 1715	40 25.4	1 56.9	60
BII-6	Jul 31 1987	1287 1329	40 54.7	2 11.5	55
BII-8	Aug 1 1987	1295 1357	41 02.6	2 27.8	59
BIII-3	Jun 25 1988	1774 1783	40 18.5	1 57.2	33
BIII-4	Jun 26 1988	2163 2039	40 37.7	3 06.2	16
BIII-5	Jun 26 1988	2256 2239	40 32.3	3 44.7	80

The object of this paper is to provide new and detailed information on the diet of *Bathypterois mediterraneus* from depths of 1000–2250 m in the western Mediterranean. Its feeding habits are analyzed in different bathymetric strata and within groups of immature and adult specimens. The influence of these factors on diet, and patterns of dietary overlap, are also discussed.

## Materials and methods

Samples were collected from the continental slope (1000–2250 m) of the Catalan Sea (western Mediterranean), during two cruises (BATHOS II–III), on board the RV *García del Cid* (Table 1), with a semi-balloon otter-trawl (OTSB14) towed from a single warp (cf. Merret and Marshall, 1981).

All specimens were fixed in 10% formalin immediately after capture. Once in the laboratory, they were measured (standard length: SL, to the nearest millimeter) and dissected to analyze the gut contents. A total of 305 specimens were dissected to examine feeding activity.

The linear and poorly differentiated stomach of *Bathypterois mediterraneus* is almost always found empty; prey are usually found in the intestine. Therefore, intestinal contents were analyzed, which makes identifying prey more difficult, because of advanced digestion.

Food items were identified to the lowest taxonomic level possible. Numbers and weights were registered to the nearest 0.1 mg, after items were dried with blotting paper to remove surface moisture.

The quantitative importance of each prey group in the diet was determined by the index of relative importance (IRI) (Pinkas et al., 1971), defined as

$$IRI = \%F(\%N + \%V),$$

where  $\%F$  = frequency of occurrence of the food item;

$\%N$  = numerical percentage of a food item in the stomachs; and

$\%V$  = percentage by volume of the food item in the stomachs (Hureau, 1970).

In our study, weight was used ( $\%W$ ) instead of volume ( $\%V$ ). This modified index has been expressed as  $\%IRI = (IRI/\Sigma IRI) \times 100$  (Rosacchi and Nouaze, 1987).

To analyze the diet of *Bathypterois mediterraneus*, individuals from all trawls were grouped according to capture depth (three bathymetric strata: 1000–1425 m; 1425–1800 m; and 1800–2250 m) and size of individuals (two categories: immature or size 1, standard length <113 mm; and mature or size 2, standard length  $\geq$ 113 mm). The  $\%IRI$  of the main prey items was determined for each of the six combinations of depth and size by pooling diet data from the individuals included in each combination. The affinity of these six combinations was computed by using a hierarchical analysis (weighted-pair groups methods analysis, WPGMA).

Trophic diversity ( $H$ ) was calculated, in terms of mean  $\%W$  of prey items, by using the Shannon index. Degree of overlap in the diet of *Bathypterois mediterraneus*, by different sizes and bathymetric strata, was determined, based on mean  $\%W$  results, by using the quantitative Schoener index (Schoener, 1974).

## Results

Of the 305 specimens of *Bathypterois mediterraneus* analyzed, 23 had an empty gut. Forty-nine categories of prey items were identified from the 282 guts containing food (Table 2). Calanoid copepods were the most numerically abundant prey ( $\%N=81.11\%$ ), and mysids were the most abundant by mass ( $\%W=37.59\%$ ). Calanoid copepods ( $\%IRI=91.63$ ), according to Wishner (1980) and Smith (1982), are planktonic elements of the benthopelagic fauna. Benthic fauna are accidental prey.

From the cluster analysis of the size and depth combinations, we identified four groups (Fig. 1): juveniles collected at depths of 1800–2250 m (group A), adults collected at

this depth (group B), adults and juveniles from other two depth categories (groups C and D).

### Group A, juveniles (size 1) from 1800–2250 m

In 68 specimens analyzed, benthopelagic calanoid copepods (Table 2) were the most important prey (%*IRI*=56.26). Benthic tanaidaceans were secondary (Fig. 2A), despite having a low overall weight, because they were frequently captured (*Wspecimen*=0.0001 g). Amphipods were the most abundant accidental prey item (%*IRI*=15.27) owing mainly to the weight of *Rhachotropis* sp. and other amphipods (Fig. 2A).

### Group B, adults (size 2) from 1800–2250 m

Calanoid copepods predominated in the 25 adult specimens analyzed (%*IRI*=79.52), whereas suprabenthic mysids were

secondary because of their high weight (Fig. 2B). Benthic cumaceans were the major accidental prey (%*IRI*=9.6) because of high numerical abundance (Fig. 2B).

### Group C, 1425–1800 m

In 95 specimens analyzed, the most important prey were benthopelagic calanoid copepods; their high frequency and abundance (Fig. 3) resulted in a %*IRI* of 95.49%. Incidence of other prey was minimal, %*IRI* <1.5.

### Group D, 1000–1425 m

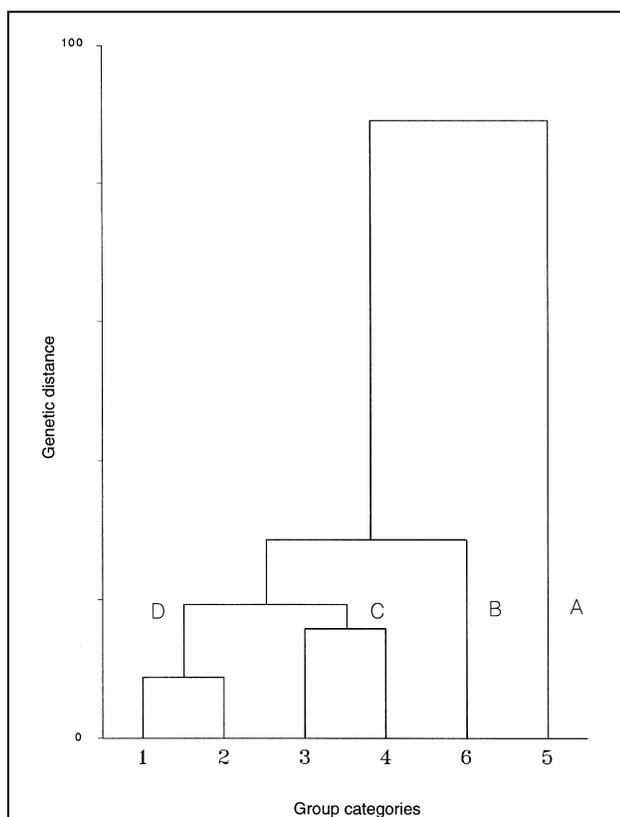
In 94 specimens analyzed, planktonic benthopelagic calanoid copepods were the most important prey (%*IRI*=88.72). Suprabenthic mysids were the major accidental prey because of their high mass (%*W*=43.11 %) (Fig. 4).

Trophic diversity values (*H'*, Table 2) were lowest at depths of 1425–1800 m, highest in adults from 1800 to 2250 m, and higher in adults than juveniles for all the bathymetric zones analyzed. Dietary overlap (Table 3) was higher between groups 1000–1425 m and 1425–1800 m. Affinity between the diets of juveniles from 1800 to 2250 m and all other groups was low.

## Discussion

According to Sulak (1977), *Bathypterois* species feed on benthopelagic plankton. Our study shows that *Bathypterois mediterraneus*, on the deep slope in the Catalan Sea, feed mostly on benthopelagic plankton (calanoid copepods), although occasionally on benthic resources (mainly suprabenthic form; occasionally endobenthic cumaceans, tanaidaceans, etc; or epibenthic amphipods). The long and thin laminar gill rakers of *Bathypterois mediterraneus* (Carrasón and Matallanas, 1994) are highly adapted for retaining planktonic prey and indicate filter feeding. Munk (1965) noted that *Bathypterois* have minute eyes, probably of limited use in feeding. However, Collin and Partridge (1996) suggest that *Bathypterois dubius* may use two retinal area specializations in feeding. *Bathypterois mediterraneus* may exhibit similar behavior. However, there are no photographs of *Bathypterois* with an open mouth that might confirm filter feeding. The small size of *Bathypterois mediterraneus* is important in its feeding because Sulak (1984b) postulated that small-bodied components of the abyssal fauna are microphagous (e.g. *Bathypterois longipes*).

Bathymetric differences were found in the diet of *Bathypterois mediterraneus*. The prey consumed changed with depth, mainly at 1800–2250 m, where juveniles, in addition to benthopelagic calanoid copepods, also fed on endobenthic and epibenthic prey, mostly tanaids (80% of them found in individuals from a catch at a depth of 2250 m). Although a sample taken at 1800 m did not indicate a greater abundance of tanaids than in shallower waters (800–1000 m) (Cartes<sup>1</sup>), it is probable that tanaid abun-



**Figure 1**

Dendrogram of dissimilarity between diets of different groups (bathymetric and ontogenetic) of *Bathypterois mediterraneus*. 1=immature (size 1) individuals of 1000–1425 m depth; 2=mature (size 2) individuals of 1000–1425 m depth; 3=immature (size 1) individuals of 1425–1800 m depth; 4=mature (size 2) individuals of 1425–1800 m depth; 5=immature (size 1) individuals of 1800–2250 m depth; 6=mature (size 2) individuals of 1800–2250 m depth. Groups identified: A = 5; B = 6; C = 3, 4; and D = 1, 2.

<sup>1</sup> Cartes, J. 1998. Personal commun. Institut Ciències del Mar (CSIC), P. Joan de Borbó s/n, 08039 Barcelona, Spain.

**Table 2**

Composition of the diet of *Bathypterois mediterraneus* in the four groups (bathymetric and ontogenetic) established. IRI = index of relative importance; %IRI = percentage of IRI. Unid. = unidentified.

	1000–1425 m		1425–1800 m		1800–2250 m			
	(Sizes 1 and 2)		(Sizes 1 and 2)		Size 1		Size 2	
	2.69		2.33		2.87 (2.93)		3.16	
No. of specimens with food	94		95		25		68	
Composition of diet	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Foraminifera	—	—	0.3	0.0	—	—	—	—
Polychaeta	75.0	0.6	4.6	0.0	29.4	0.3	42.4	0.3
Polychaeta unid.	41.5	0.4	1.2	0.0	—	—	25.0	0.2
Aphroditomorfa	4.2	0.0	1.1	0.0	29.4	0.3	4.2	0.0
Crustacea								
Crustacea unid.	42.0	0.4	—	—	—	—	—	—
Copepoda	9966.3	77.4	13195.5	90.0	5644.8	52.2	8550.2	67.6
Copepoda unid.	—	—	8.4	0.1	—	—	—	—
Calanoid Copepoda	9966.3	88.7	12531.0	95.5	5014.3	56.3	8550.2	79.5
Harpacticoid Copepoda	—	—	—	—	37.3	0.4	—	—
Ostracoda	20.0	0.2	3.8	0.0	—	—	3.4	0.0
Ostracoda unid.	0.9	0.0	0.1	0.0	—	—	0.4	0.0
Cipridina sp.	—	—	1.0	0.0	—	—	1.5	0.0
Cipridinidae	12.4	0.1	0.4	0.0	—	—	—	—
Amphipoda	609.5	4.7	117.1	0.8	1651.2	15.3	516.5	4.1
Amphipoda unid.	—	—	0.4	0.0	—	—	0.8	0.0
Amphipoda Gammaridea	551.2	4.3	95.2	0.7	1651.2	15.3	477.5	3.8
Amphipoda Gammaridea unid.	138.1	1.2	30.2	0.2	151.8	1.7	122.8	1.1
<i>Orchomene humilis</i>	15.5	0.1	—	—	—	—	—	—
<i>Orchomene</i> sp.	—	—	0.1	0.0	13.6	0.2	—	—
Lyssianasidae	17.8	0.2	3.0	0.0	26.6	0.3	—	—
<i>Harpinia</i> sp.	—	—	1.0	0.0	—	—	—	—
<i>Bruzelia typica</i>	—	—	2.5	0.0	—	—	4.7	0.0
<i>Pseudotiton bouvieri</i>	—	—	—	—	—	—	0.7	0.0
<i>Rhachotropis caeca</i>	0.7	0.0	—	—	—	—	—	—
<i>Rhachotropis</i> sp.	14.7	0.1	—	—	438.3	4.9	30.6	0.3
<i>Monoculodes</i> sp.	0.9	0.0	—	—	—	—	0.9	0.0
Oediceridae	—	—	—	—	—	—	3.9	0.0
Amphipoda Hyperiidea	1.3	0.0	0.2	0.0	—	—	—	—
Isopoda	13.1	0.1	5.0	0.0	22.6	0.2	8.8	0.1
Isopoda unid.	1.3	0.0	2.2	0.0	5.7	0.1	2.9	0.0
<i>Gnathia</i> sp.	1.0	0.0	—	—	—	—	0.4	0.0
Anthuridae	1.0	0.0	0.6	0.0	5.7	0.1	0.3	0.0
<i>Ilyarachna</i> sp.	0.2	0.0	—	—	—	—	—	—
Tanaidacea	0.9	0.0	7.7	0.1	2664.1	24.6	49.5	0.4
Tanaidacea unid.	0.9	0.0	—	—	—	—	—	—
Tanaidae	—	—	7.7	0.1	2664.1	29.9	41.7	0.4
Paratanaidae	—	—	—	—	—	—	0.3	0.0
Cumacea	15.8	0.1	194.6	1.3	751.8	7.0	1214.7	9.6
Cumacea unid.	7.3	0.1	99.3	0.8	401.9	4.5	596.0	5.5
<i>Cyclaspis longicaudata</i>	—	—	0.6	0.0	—	—	14.0	0.1
<i>Leucon longirostris</i>	0.6	0.0	—	—	—	—	—	—
<i>Campylaspis glabra</i>	0.2	0.0	—	—	—	—	—	—
<i>Campylaspis</i> sp.	—	—	0.1	0.0	—	—	—	—

continued

Table 2 (continued)

	1000–1425 m		1425–1800 m		1800–2250 m			
	(Sizes 1 and 2)		(Sizes 1 and 2)		Size 1		Size 2	
	2.69 94		2.33 95		2.87 (2.93) 25		3.16 68	
Composition of diet	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Nannastacidae	—	—	1.6	0.0	—	—	—	—
<i>Platysympus typicus</i>	—	—	2.2	0.0	65.6	0.7	14.7	0.1
<i>Diastylis</i> sp.	—	—	0.2	0.0	7.6	0.1	9.1	0.1
<i>Makrokyllindrus</i> sp.	—	—	—	—	—	—	9.4	0.1
Mysidacea	2112.3	16.4	1078.8	7.4	50.3	0.5	2269.5	17.9
Mysidacea unid.	785.5	7.0	196.0	1.5	50.3	0.6	1117.3	10.4
<i>Boreomysis arctica</i>	108.4	1.0	47.0	0.4	—	—	2.2	0.0
<i>Boreomysis</i> sp.	49.3	0.4	148.9	1.1	—	—	198.2	1.8
<i>Parapseudomma</i> sp.	1.2	0.0	—	—	—	—	—	—
Decapoda	4.3	0.0	27.9	0.2	—	—	—	—
Decapoda unid.	4.3	0.0	—	—	—	—	—	—
Larval Decapoda	—	—	0.4	0.0	—	—	—	—
Decapoda Natantia	—	—	17.4	0.1	—	—	—	—
<i>AcanthePHYRA eximia</i>	—	—	7.2	0.1	—	—	—	—
<i>Pontophilus norvegicus</i>	—	—	1.5	0.0	—	—	—	—
Osteichthyes	—	—	27.0	0.2	—	—	—	—
Scales	16.0	0.1	—	—	—	—	—	—

dance increases in the environment at 2250 m. The mouth position of *Bathypterois* makes it improbable that they can extract tanaids from the substratum, in which these creatures tend to live. Holdich and Jones (1983) observed that some tanaids can swim very fast for short periods and it is probable that *Bathypterois mediterraneus* capture them during these periods. At 1800–2250 m, adult *Bathypterois mediterraneus* consume mysids as secondary prey, which they capture swimming over the bottom.

The scarcity of resources, which decrease even more below 1200–1400 m (Cartes and Sorbe, 1993), may force *Bathypterois* to diversify their diet at 1800–2250 m ( $H=2.93$ ), extending to endobenthic prey, such as cumaceans and tanaidaceans. This stenophagic decrease coincides with Dayton and Hessler's (1972) deep predator prototype. Less intense specialization in a type of resource leads deep predators to be more adaptable, whether due to a general scarcity of resources or to the abundance of an occasional single resource.

Ontogenetic differences in the diet were small. Adult intestines mainly contained more and larger prey than did the intestines of juveniles, from all depths. Only at 1800–2250 m were there clear differences in the prey captured by juveniles and adults, possibly reflecting pronounced qualitative changes in the decapod fauna of the western Mediterranean recorded around 2000 m by Cartes (1993d). *Bathypterois grillator*, the largest member of the genus (Sulak, 1977) from the Bahamas, also has an ontogenetic shift in diet (Crabtree et al., 1991), but *Bathyp-*

Table 3

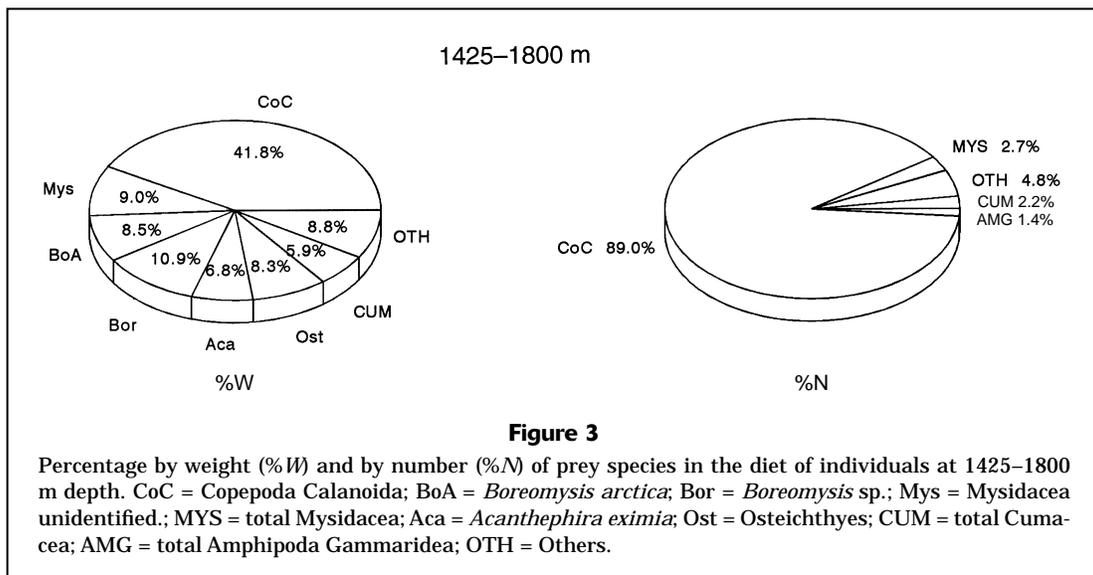
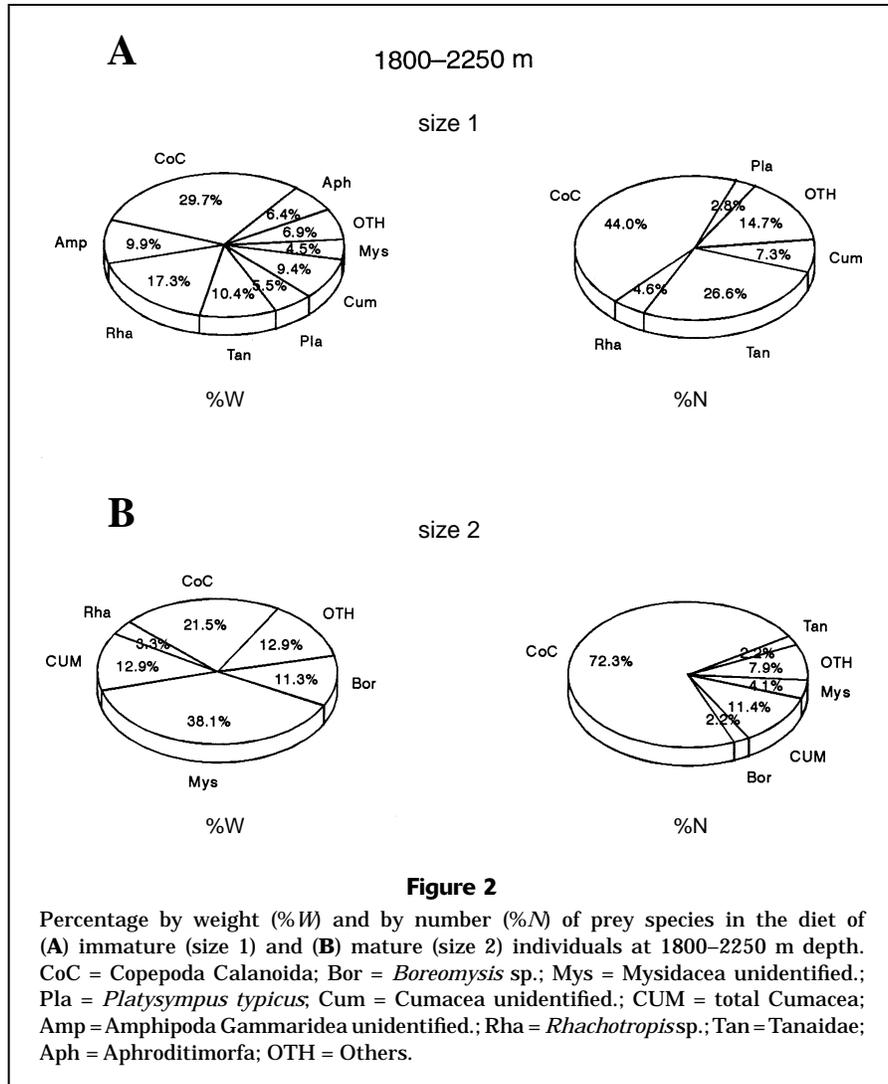
Diet overlap (Schoener index) among the different bathymetric and ontogenetic groups established.

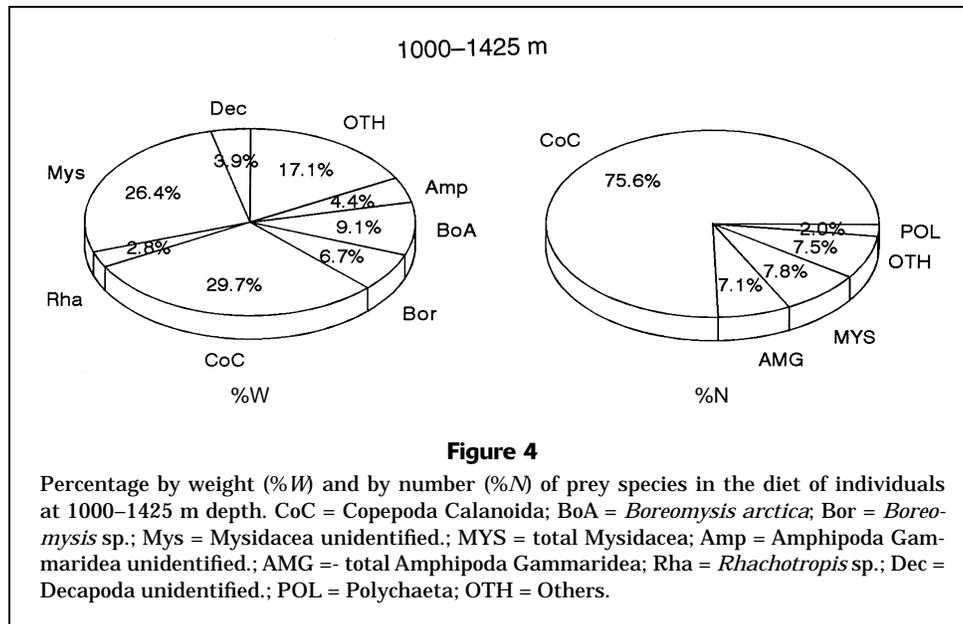
	1425–1800 m		1800–2250 m	
	Sizes 1 and 2	Size 1	Size 2	
1000–1425 m	0.70	0.50	0.69	
1425–1800 m	—	0.47	0.65	
1800–2250 m. (size1)	—	—	0.60	

*ois longipes* and *Bathypterois phenax* do not significantly shift their diet ontogenetically.

Our study goes beyond the preliminary data of Carrassón and Matallanas (1990), indicating that benthopelagic plankton, namely calanoid copepods, play an important dietary role in *Bathypterois mediterraneus*. Further, greater importance for mysids over amphipods (both accidental prey), coincided with their relative abundance in the area (Cartes and Sorbe, 1993). Tanaids were found in the diet for the first time and seem important at depths of 1800–2250 m.

*Bathypterois dubius*, a related species found in the North Atlantic has a diet broadly similar to that of *Bathypterois mediterraneus* feeding exclusively on planktonic copepods (Marshall and Merrett, 1977). However, Sal-





danha (1988) reported that *Bathypterois dubius* consumes some amphipods and mysids in addition to calanoid copepods, a finding similar to our data for *Bathypterois mediterraneus*. In the western North Atlantic (Crabtree et al., 1991) and eastern North Atlantic (Marshall and Merret, 1977; Merret, 1987) *Bathypterois longipes* primarily feed on copepods, amphipods, and decapods, but the difference is the greater importance of the benthic prey for *Bathypterois mediterraneus*, especially at depths between 1800 and 2250 m.

In the Atlantic, *Bathypterois dubius* is restricted to depths of less than 2000 m (Sulak, 1984a); *Bathypterois longipes* inhabits depths below 2000 m. Sulak (1977) considered the bathymetric and geographic distribution of these species to be a consequence of competitive interspecific exclusion, and this is supported by the results of Marshall and Merrett (1977). *Bathypterois mediterraneus* is the only abundant Mediterranean species of *Bathypterois*, with a lower bathymetric limit of 2800 m (Bauchot, 1987). In the Catalan Sea, it ranges down to the maximum depth of 2250 m and exclusively exploits a trophic niche unoccupied by any other species. This strategy enables *Bathypterois mediterraneus* to be the dominant species below 1425 m, where resources are more limited.

The relatively higher metabolism as a result of small size in *Bathypterois mediterraneus*, like other *Bathypterois* (Heezen and Hollister, 1971; Saldanha, 1977), is compensated by reduced mobility and coupled with a microphagous filtering diet based on organisms distributed more uniformly in space, such as calanoid copepods. This trophic strategy makes *Bathypterois mediterraneus* especially fit for a nutrient-limited environment, such as the Mediterranean, particularly at greater depths (Carpine, 1970; Thiel, 1983; Pérès, 1985).

*Bathypterois* species are dominant on the middle and lower slope and in the abyssal depths of oligotrophic regions or similar less productive water masses. Sulak (1984b)

and Merrett (1987) have noted the major importance of Chlorophthalmidae in marine fauna of oligotrophic environments. In more productive water masses, species with energetically expensive life history patterns dominate the ichthyofauna. In the Mediterranean, changes in biomass are evident so that the larger and middle-size dominant species between 1000 and 1200 m (*Mora moro*, *Phycis blennoides*, *Trachyrhynchus trachyrhynchus*, and *Alepocephalus rostratus*) are progressively replaced at greater depth by other smaller species such as *Bathypterois mediterraneus*, *Coryphaenoides guentheri*, and *Chalinura mediterranea* (Stefanescu et al., 1993). The relative importance of *Bathypterois mediterraneus* increases as depth increases (Stefanescu et al., 1993), parallel to an increasing scarcity of trophic resources (Cartes, 1991; Cartes and Sorbe, 1993). This species is the most abundant fish of the lower slope assemblage (Morales-Nin et al., 1996) and exemplifies a species adapted to a food scarce environment by energetically conservative feeding strategies.

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